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AUTHOR(S):

Takahashi, Tetsumi; Ota, Kazutaka; Kohda, Masanori; Hori, Michio

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Some evidence for different ecological pressures that constrain male and female body size

Tetsumi Takahashi^{1*}, Kazutaka Ota¹, Masanori Kohda² and Michio Hori¹

(1) Laboratory of Animal Ecology, Graduate School of Science, Kyoto University,
Kitashirakawa-Oiwake, Sakyo, Kyoto 606-8502, Japan

(2) Laboratory of Animal Sociology, Graduate School of Science, Osaka City University,
Osaka 558-8585, Japan

*Tetsumi Takahashi

Email: tetsumi@terra.zool.kyoto-u.ac.jp

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Abstract The dwarf morph of the Lake Tanganyika cichlid *Telmatochromis temporalis* uses empty snail shells as shelters and breeding sites in shell beds, in which many empty shells exist. Here, we assessed selection forces regulating body size in this fish. Field observations showed that large males tended to have a greater number of females in their territories, suggesting that sexual selection favours large males. Nonetheless, a transplant experiment suggested that male body size was limited by the ability to hide in empty shells from large piscivorous fish. In females, the number of ovarian eggs increased with body size, suggesting that fecundity selection favours large females. However, females are smaller than males. Females spawned eggs close to the apices inside the shells. The small space there would decrease the risk of egg predation by egg predators, and small body size of females may be a result of adaptation to spawn eggs in the small, safe spaces. The present study provides support for the idea that male and female body sizes have been limited by different ecological pressures (predation on adult fish in males, predation on eggs in females), which has not been reported previously in any animal.

Introduction

Body size results from a balance between selection favouring large body size and counterbalancing selection favouring small body size (e.g. Schluter et al., 1991; Blanckenhorn, 2000, 2005). Sexual selection in males and fecundity selection in females are widely agreed to be the major evolutionary forces that favour larger body size (e.g. Heske and Ostfeld, 1990; Webster, 1992; Forsgren et al., 1996; Székely et al., 2000 for sexual selection, and Elgar, 1990; Head, 1995; Prenter et al., 1999 for fecundity selection). However, evidence of counterbalancing selection limiting body size is still sparse and requires more research (Blanckenhorn, 2000, 2005).

Selection limiting body size is generally attributed to internal constraints (e.g. limitation of physiological traits such as metabolic rate, Peters and Wassenberg, 1983; Demment and Van Soest, 1985; Hughes and Hughes, 1986). External (ecological) pressures acting on phenotypes, for example, predation and limitation of resources, are well known as a major force in the evolution of organisms (e.g. Schluter, 2000), but their role in limitation of body size is surprisingly not well known. Taking sex into account, the ecological limitation of body size can be classified into three types.

Type 1: an ecological pressure limits body size in one sex, and other forces, e.g. physiological constraints, restrict body size in the other sex. If optimal body size or strength is different between ecological pressure on one sex and other forces on the other sex, it may accelerate evolution of sexual size dimorphism (SSD). In a population of *Lamprologus callipterus* (cichlid fish) from Lake Tanganyika, which shows the most extreme male-biased SSD (males > females) among animals (Schütz and Taborsky, 2000), the body size

of females appears to be restricted by the ability to spawn eggs inside empty snail shells of a gastropod. Mature males of this species (except for sneakers) are too large to enter shells, and no ecological pressures limiting body size have been reported, although the large body size may be a result of sexual selection and natural selection so that the males could carry the shells with their mouths to make breeding nests (Schütz and Taborsky 2005; Schütz et al., 2006). In raptorial birds that exhibit female-biased SSD (females > males), male body size may be limited by the ability to capture small, abundant prey (Safina, 1984). Small males would be more successful in breeding through courtship feeding. In females, no evidence has been reported for ecological pressures that restrict body size.

Type 2: an ecological pressure limits body size in both sexes. Such an ecological pressure may regulate body size to be equal between the sexes. Indeed, maximum body size of a bruchid beetle appears to be equal between sexes because the body size is limited by the ability to escape from fruit that does not dehisce through the fruit's apical pore (this selection does not work when fruit dehisces, Ott and Lampo, 1991). However, an ecological pressure common to the sexes may have caused SSD in small mustelids. The diameter of the body of these animals appears to be limited by the diameter of burrows of their basic prey species (Simms, 1979; Erlinge, 1987). Since female body diameter increases during pregnancy, females must be thinner when non-pregnant, and in consequence much smaller (Gliwicz, 1988). In some other animals, positive or negative effects of environment on body size (e.g. temperature, food availability, water current, and others) have been reported in both sexes (e.g. Plaistow et al., 2004 in soil mites, Uhl et al., 2004 in cellar spider, Stearns et al., 2000 in fruit fly, Tracy, 1999 in chuckwalla, Wapstra et al., 2001 in skink, Jonsson et al., 2001 in brown trout, Reznick and Ghalambor 2005; Hendry et al., 2006 in guppies, and Walsh and Reznick, 2008 in Killifish). A well-known

theory connecting environments with body size explains that early maturity, namely, small body size, is favourable under strong ecological pressures because it can increase probability of surviving to maturity (e.g. Stearns, 1992). Some of the studies listed above support this theory.

Type 3: an ecological pressure limits body size in one sex, and a different ecological pressure limits body size in the other sex. If optimal body size or strength is different between ecological pressures acting on males and females, it may result in SSD. Such ecological pressures are theoretically possible, and will possibly be common in animals, but no examples have been reported. The present study provides evidence for this scenario in a fish.

Telmatochromis temporalis is a substrate-brooding cichlid belonging to the tribe Lamprologini in Lake Tanganyika, Africa (Takahashi, 2003). The dwarf morph of this species exhibits male-biased SSD (Table 1, Fig. 1), but no sexual differences in body shape are found (Takahashi, 2004). This morph invariably inhabits shell beds (i.e. high-density accumulations of empty snail shells of the gastropod *Neothauma tanganyicense*). In the shell beds, only small openings exist (< 17 mm in diameter), and these openings mainly consist of spaces within the shells and under fragments of broken shells. The dwarf morph uses the shells as shelters and spawning sites. The normal morph of this species is common on rocky shorelines, and takes refuge in spaces under stones to avoid predation by piscivorous fish (Hori, 1997; Hori et al., 1993). Small reproductively parasitic males (sneakers) are reported in the normal morph (Katoh et al., 2005), but not in the dwarf morph.

At the southern end of the lake, shell beds and dwarf morph populations exist in two areas, namely, Chibwensolo and the Nkumbula-Wonzye area. A molecular phylogenetic study suggested that the dwarf morph evolved from the normal morph independently in these areas (Takahashi et al., 2009). Since the body size of the dwarf morph is much smaller than that of the normal morph in both sexes (Table 1), selection limiting body size has probably played important roles in the evolution of the dwarf morph. In the present study, we conducted 1) behavioural observations to examine whether sexual selection favours large body size in males, 2) observations of ovarian eggs to examine whether fecundity selection favours large body size in females, 3) a transplant experiment to assess an ecological pressure limiting body size of males, and 4) observations of spawning sites inside shells to assess an ecological pressure limiting body size of females.

Materials and Methods

Study sites

This study was conducted at Wonzye near Mpulungu, Zambia, at the southern end of Lake Tanganyika (8°44'S, 31°08'E) using SCUBA-diving. At Wonzye, a rocky bottom extends between 0 and 5 m in depth. A sandy bottom expands at greater depths beyond the rocky shoreline (> 5 m in depth). A rocky ridge (about 3 m in height, about 10 to 20 m in width) extends from the rocky shoreline and beside a shell bed that expands on the sandy bottom at 10 m in depth. The dwarf morph is abundant in the shell bed, but not found on the rocky shoreline or the rocky ridge. The normal morph is abundant on the rocky shoreline, and rare

on the rocky ridge. Young of the normal morph are also found in the shell bed. The dwarf and normal morphs are not found on the sandy bottom.

Fish size and shell size

To gain basic data regarding the relationships among fish size, shell size, and fish sex, we collected fish in September to December of 2005, December 2006, and August to September of 2010. The fish went in and out of particular empty shells repeatedly. These shells were regarded as the shelters of the fish. The standard length (SL) of the fish (distance from the anterior tip of the upper jaw to the midpoint of the origin of the caudal fin) and the height of the shell (distance from the apex to the outer part of the lip) were measured with callipers under a binocular microscope to the nearest 0.1 mm, and the sex of the fish was determined from the shape of the genital papilla. Maturity of fish was determined from their body size (Takahashi et al., 2009), and only mature males (> 25 mm SL, $N = 56$) and mature females (> 17 mm SL, $N = 76$) were used for the analysis.

Behavioural observations

To assess whether sexual selection acts on male body size, we compared three variables, (1) body size of a territorial male, (2) number of empty gastropod shells in the territory of the male, and (3) number of females in the territory of the male. Behavioural observations were carried out in the shell bed from October to December 2007. Two quadrats (2 m x 5 m) divided into 40 grids (0.5 m x 0.5 m) were set on the bottom to facilitate mapping

(separated from each other by a distance of 10 m). We made substrate maps of the quadrats, and recorded all empty gastropod shells on the maps. Large males remained in particular areas, and aggressively chased other individuals from these areas when they met. These defended areas were defined as the territories of the males. However, the males did not chase some females that remained near particular empty shells located in the males' territories. A male and these nearby females were regarded as a breeding unit.

We observed all breeding units found in the quadrats ($N = 17$). We recorded the swimming tracks of the males for 20 minutes per breeding unit, and counted the females in the territories of the males. After the observations, we measured the SLs of the fish with a ruler to the nearest 1 mm, and confirmed from the shapes of the genital papillae that each breeding unit was composed of a large aggressive male and some small females. The shells in each territory were counted from the substrate maps. The dwarf morph feeds mainly on algae that grow on the surfaces of the shells and the fragments of broken shells. Indeed, the 17 males that we observed pecked at algae 34.9 times on average during a 20-min period. However, algae appear to be abundant in the males' territories, and intra- and inter-sexual competition for algae is probably not very strong. Therefore, food was not considered in this analysis.

Female size and number of ovarian eggs

To assess fecundity selection, we reanalysed 174 female samples that were used in Takahashi (2010): these fish were collected at the shell bed in Wonzye between September and December of 2005, and preserved in 100% ethanol. In the female dwarf morph, the

ovarian eggs consist of two size groups (Takahashi, 2004). The dwarf morph is iteroparous, and the number of large, developed ovarian eggs is thought to be equal to the number of eggs that a female spawns at once. The number of large ovarian eggs was counted for 64 females whose small and large ovarian eggs were easily identified by visual inspection (the large ovarian eggs were > 1 mm in diameter, whereas the small ovarian eggs were < 0.5 mm in diameter). We call the “large ovarian eggs” simply “ovarian eggs” below. The SL of fish was measured with callipers under a binocular microscope to the nearest 0.1 mm.

A transplant experiment

To estimate maximum body size of individuals that can enter the shells, we conducted a transplant experiment in October to December of 2006 and April to May of 2007. This experiment required the release of individuals with body sizes ranging from small (able to enter shells) to large (unable to enter shells). Therefore, we used males of the normal morph. The normal morph individuals of various sizes were captured on the rocky shoreline ($N = 43$, 21–68 mm SL). The SLs of fish were measured with a ruler to the nearest 1 mm. Then 22 (21–68 mm SL) out of the 43 individuals were transported to a release site in the shell bed, where only small openings (< 17 mm in diameter of the mouth, Takahashi et al., 2009) are available for fish to hide in. The remaining 21 individuals (24–67 mm SL) were transported to a site different from the capture site on the rocky shoreline, where variously sized openings (large openings are larger than 80 mm in diameter of the mouth, Takahashi et al., 2009) are available for fish to hide in. Each individual was covered with a cage (43 cm x 34 cm x 26 cm). Twenty-four to 120 hours (usually 48 hours) after the transportation, the fish fed on algae in the cages, and appeared to be accustomed to the new surroundings.

Then, the cage was removed in the daytime, and the behaviour whether a released individual entered openings was observed for 20 min.

Positions of eggs in shells

To examine the positions where females deposit eggs inside shells, we sampled shells containing females (i.e. potentially brood-caring females) in the shell bed in August and September of 2010. Because the breeding positions inside shells are invisible from the outside, we broke the sampled shells with a diving knife under water. When eggs were adhering to the inside wall of a shell, we transported the broken shell with the eggs and the female to the laboratory at Mpulungu ($N = 16$). We measured the diameter of the space inside the shell where the eggs were adhering (the length of the longest axis of the cross-section of the space) and the SL of the female with callipers under a binocular microscope to the nearest 0.1 mm.

Statistics

Comparisons between two variables (e.g. fish size and shell size) were performed using Pearson's test (Sokal and Rohlf 1995). In these analyses, log transformations were used so that linear models could be applied. The difference in body size between the sexes was tested by the Mann-Whitney U test, implemented in JMP 6.0.2. In the transplant experiment, the behaviours (entering openings and not entering openings) were fitted to a logistic regression, and likelihood ratio test between nested models was performed to assess

significance in JMP. Two-tailed tests were applied for all statistical tests. The Bonferroni correction (Rice, 1989) was used when multiple comparisons were made.

Results

Fish size and shell size

The size range of shells used by males was 38.6–53.2 (mean \pm standard deviation = 45.2 ± 3.2) mm in height, and the size range of shells used by females was 28.1–51.1 (40.8 ± 4.2) mm in height (Fig. 2). Shell sizes were significantly different between sexes of the fish (Mann-Whitney U test: $z = 5.9$, $P < 0.001$). The shell size was not significantly correlated with body size in either sex (Fig. 2).

Behavioural observations

A total of 17 breeding units were recognized. The body size of the territorial males was 29–35 (32.6 ± 1.7) mm SL. The number of females per breeding unit was one to six (2.3 ± 1.4 , $N = 39$ in total). The body size of these females was 18–25 (22.0 ± 1.4) mm SL. The body sizes of these males and females fell within the size ranges of the mature males and mature females, respectively (Takahashi et al., 2009). The territories of males did not overlap. A total of 8–41 (22.6 ± 9.7) shells were distributed in these territories.

In the Pearson's tests (Table 2), male body size was positively correlated with the number of shells in the territory, and the latter was positively correlated with the number of females in the breeding unit. This suggests an indirect positive correlation between male body size and the number of the females via the number of shells in the territory, although a direct correlation between these variables was not detected.

Female size and number of ovarian eggs

The body size of the 64 females examined was 17.3–26.0 mm SL, and the number of ovarian eggs was 4–18. The number of ovarian eggs increased significantly with increasing female body size (Fig. 3).

The transplant experiment

The behavioural pattern of released fish was clearly different between the shell bed and the rocky shoreline (Fig. 4). In the shell bed, 11 small released individuals (21–47 mm SL) remained near particular empty shells, went in and out of the shells repeatedly, and dashed into the shells when a large piscivorous fish (*Lepidolamprologus cunningtoni*) approached. In contrast, 11 large individuals (39–68 mm SL) swam around without entering any openings, and *L. cunningtoni* chased these individuals when they met (2.0 ± 2.3 times during a 20-min period, $N = 11$). These alternative behavioural traits (entering openings and not entering openings) were significantly associated with the body size of the released individuals (Fig. 4a).

In the rocky shorelines, 17 out of the 21 released individuals (24–65 mm SL) remained near particular spaces under stones, and went in and out of the spaces repeatedly. Three large released individuals (47–67 mm SL) swam around, and entered several spaces under stones while swimming. Only one released individual (53 mm SL) swam around without entering any openings. The relationship between body size and behaviour (entering openings and not entering openings) was not significant in the released individuals (Fig. 4b).

Positions of eggs in shells

Sixteen shells contained 1–12 (6.8 ± 3.0) eggs with a female. The body size of the 16 females was 18.6–24.8 (21.7 ± 1.9) mm SL; these body sizes fell within the size range of mature females (Takahashi et al., 2009). The eggs were adhering to the inside walls of the shells close to the apices. The diameter of the inner space in the shell to which the eggs were adhering was 7.1–11.5 (9.0 ± 1.1) mm. The diameter of this space of the shells was positively correlated with female body size (Fig. 5).

Discussion

Male body sizes

Many animal species with a polygynous mating system show pronounced sexual dimorphism, with males typically being larger than females, and this phenomenon is

generally attributed to sexual selection on male size (e.g. Heske and Ostfeld, 1990; Webster, 1992; Székely et al., 2000; Tobler et al., 2008). The dwarf morph of *T. temporalis* was also highly polygynous (six females were found in a male's territory in the maximum case), and larger males tended to have more females in their territories. Thus, sexual selection on male body size may be intense. However, the male dwarf morph is much smaller than the males of the ancestral normal morph and many other Lamprologini species (Table 1; Poll, 1956). Thus, strong selection pressure for small body size presumably acts on the males.

In the field transplant experiment, large individuals of the normal morph that were released in the shell bed did not enter openings (Fig. 4a). This phenomenon was more likely a result of their large body size than a behavioural trait peculiar to large individuals because: (1) two large individuals (49 and 53 mm SL) attempted to enter empty shells while swimming but could not fully enter (their tails remained outside) and immediately left the shells; and (2) large released individuals (> 45 mm SL) entered openings under stones on the rocky shorelines (Fig. 4b), where many large openings exist (Takahashi et al., 2009). The proportion of released individuals that entered shells was strongly decreased for fish larger than 40 mm SL. The largest body size of the male dwarf morph coincides with this body size (the arrow "m" in Fig. 4a). The behaviour of hiding in shells from ubiquitous predators on the shell bed, i.e. *L. cunningtoni*, may have caused natural selection on the body size of the male dwarf morph. Under this selection, it might be expected that larger males would use larger shells as shelters. However, such a correlation was not observed (Fig. 2). Larger males tended to have more shells in their territories and in consequence more females (Table 2). This fact suggests that males compete with other males to gain more shells in their territories, rather than larger shells. Males presumably use the largest shells in their

territories even if these shells were larger than necessary for the males to fit into, causing the correlation between male body size and shell size to be weak.

Taken together, the above findings suggest that in the male dwarf morph, sexual selection favours large body size, but natural selection for the ability to hide in the shells limits the body size.

Female body sizes

Inter-sexual resource division to reduce competition for resources can cause SSD (e.g. Hedrick and Temeles 1989; Temeles et al., 2000; Pearson et al., 2002; Shetty and Shine 2002; Bolnick and Doebeli 2003). However, this factor may not strongly affect SSD of the dwarf morph. The average body size of mature females was 70.1% of the average body size of mature males, whereas the average size of shells used by mature females was 90.4% of the average size of shells used by mature males. These facts indicate that the shell size can explain only a part of the difference in fish size between sexes.

Large females tended to have more ovarian eggs than small females (Fig. 3). This suggests that fecundity selection favours large female size, as shown previously in many other animals (e.g. Elgar, 1990; Head, 1995; Prenter et al., 1999). On the other hand, the females spawn the eggs close to the apices inside the shells. Spawning in this small space would probably be effective in preventing predation by egg predators like carnivorous crabs (*Platythelphusa armata*), which are ubiquitous in the shell bed and juveniles to subadults of the crabs dwell in the shells (Cumberlidge et al., 1999; unpublished data of TT). Smaller

females, which spawn eggs in smaller spaces (Fig. 5), are likely to have lower risk of egg predation, although experimental studies will be needed to test this hypothesis.

The evolution of the female body size of shell-brooding cichlids has been well studied in *L. callipterus* (Schütz and Taborsky, 2000, 2005; Schütz et al., 2006). In Wonzye, this cichlid spawns eggs inside empty *N. tanganyicense* shells (Sato and Gashagaza 1997; Schütz and Taborsky 2005), as does the dwarf morph of *T. temporalis*. Three clear differences in traits associated with breeding are recognized between these shell-brooding cichlids. (1) Mature females of the dwarf morph (21.2 ± 1.3 mm SL, present study) are much smaller in body size than those of *L. callipterus* (45.8 ± 4.6 mm SL, Schütz and Taborsky 2000). (2) The dwarf morph has far fewer ovarian eggs (2–18, present study; Takahashi, 2004) than *L. callipterus* (140–238, $N = 14$, unpublished data of KO), suggesting that the dwarf morph spawns far fewer eggs as a clutch than *L. callipterus*. (3) The space that the dwarf morph deposits eggs (7.1–11.5 mm in diameter, present study) is much smaller than the space that *L. callipterus* deposits eggs (15.8–20.9 mm in diameter, $N = 17$, unpublished data of KO). These three differences suggest a trade-off between the safety of eggs and the number of eggs, namely, small females (dwarf morph) are able to spawn eggs in the small, safe spaces, but unable to spawn many eggs, whereas large females (*L. callipterus*) are able to spawn many eggs, but unable to spawn in the small, safe spaces. The linear regression obtained for the number of ovarian eggs (y) versus SL (mm) was $y = 0.74 \text{ SL} - 8.3$ in the dwarf morph ($r = 0.473$, $N = 64$, $P < 0.001$, this formula was made with non-transformed data of the present study). The slope of this line (0.74) is about one-tenth that reported for *L. callipterus* ($y = 7.8 \text{ SL} - 175.4$, $r = 0.946$, $N = 24$, $P < 0.001$, Sato, 1994). This suggests that fecundity selection is much weaker in the dwarf morph. The small effect of body size on

fecundity may cause the small body size and allow breeding in small spaces. The reasons why the effect of body size on fecundity is small are unknown.

The normal morph of *T. temporalis* and other nine substrate-brooding species of cichlid fish from Lake Tanganyika show clear lunar cyclic spawning (Nakai et al., 1990; Rossiter, 1991; Takahashi, 2010). The spawning cycles of these species are thought to improve the survival of the eggs and yolk-sac larvae by, for example, synchronizing the vulnerable stages of the brood (egg and yolk-sac stages) with the full moon, when nocturnal predators (e.g. catfish) are less active (Rossiter, 1991). However, the dwarf morph of *T. temporalis* does not exhibit lunar cyclic spawning, or at least the degree of lunar synchronization is low (Takahashi, 2010). The small spawning spaces close to the apices inside the shells will be effective for preventing predation on the eggs, and lunar cyclic spawning may be dispensable for predator avoidance (Takahashi, 2010).

Altogether, the female body size of the dwarf morph may be regulated by a balance between fecundity selection and natural selection that favours small body size so that the females can lay eggs in small, safe spaces. Inter-sexual resource (shells) division can partly explain the evolution of the small body size in females.

Conclusions

The present study of the dwarf morph of *T. temporalis* suggests that the male body size is limited by the ability to enter shells that may decrease the risk of predation on these fish by large piscivorous fish such as *L. cunningtoni*, whereas the female body size is limited by

the ability to spawn eggs inside shells close to the apices, which may decrease the risk of predation on the eggs by small carnivorous animals such as young of *Platythelphusa armata*. This study provides support for the idea that the male and female body sizes have been limited by different ecological pressures, which has not been reported previously in any animal.

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Table 1. Body size of mature individuals of *Telmatochromis temporalis* from the southern end of Lake Tanganyika. Body size was given in the mean, standard deviation, and range of the standard lengths (mm). Males with white testes and females with ovarian eggs of 1 mm or larger were regarded as the mature individuals for convenience. Data used in Takahashi *et al.* (2009) were reanalyzed. Sneaker males were not included

Locality	Sex	Normal morph	Dwarf morph
Chibwensolo	Male	67.3 ± 9.5 (56.8-88.1), <i>N</i> = 22	37.8 ± 2.7 (34.0-44.8), <i>N</i> = 25
	Female	44.2 ± 4.2 (34.9-53.6), <i>N</i> = 20	26.4 ± 1.2 (22.7-28.6), <i>N</i> = 27
Wonzye	Male	65.8 ± 6.1 (56.4-75.7), <i>N</i> = 12	30.7 ± 2.7 (25.1-40.3), <i>N</i> = 35
	Female	41.1 ± 4.5 (33.4-53.1), <i>N</i> = 24	20.8 ± 1.8 (17.2-26.8), <i>N</i> = 124

Table 2. Correlation coefficients (r) among three parameters in 17 families of the dwarf morph

	Number of shells	Number of females
Male standard length	0.559*	0.362 ^{NS}
Number of shells	—	0.728**

Pearson's test: **< 0.01, *< 0.05, ^{NS}> 0.05 after sequential Bonferroni correction

Fig. 1 The dwarf morph of *Telmatochromis temporalis* at Wonzye, Zambia. The large fish at the centre is a male, and the small fish in the shell is a female.

Fig. 2 Relationship between body size of the dwarf morph (*Telmatochromis temporalis*) and size of shells used by the fish as shelters. Solid circles indicate males, and open circles indicate females. Note \log_{10} scale used on x- and y-axes.

Fig. 3 Relationship between body size and number of ovarian eggs in females of the dwarf morph (*Telmatochromis temporalis*). Note \log_{10} scale used on x- and y-axes.

Fig. 4 Relationship between body size and behaviour in the normal morph individuals (*Telmatochromis temporalis*) that were released in (a) the shell bed and (b) the rocky shoreline. Logistic regression fitted to the proportion of fish that entered openings at each standard length. Arrows indicate the maximum body size of males (m) and females (f) of the dwarf morph.

Fig. 5 Relationship between body size of the female dwarf morph (*Telmatochromis temporalis*) and diameter of space inside shells where the fish deposited eggs. Note \log_{10} scale used on x- and y-axes.



Fig. 1

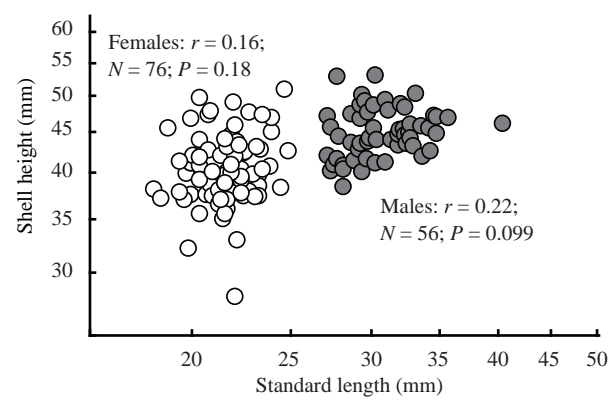


Fig. 2

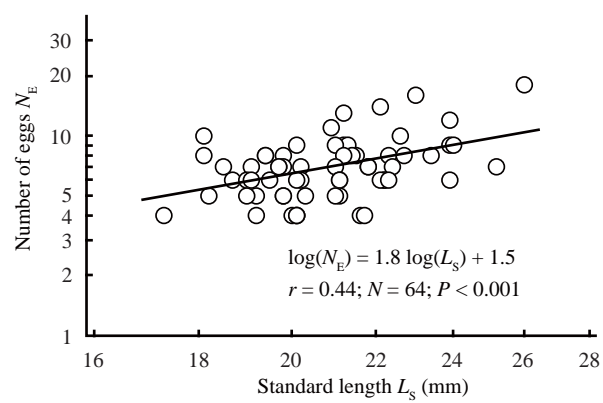


Fig. 3

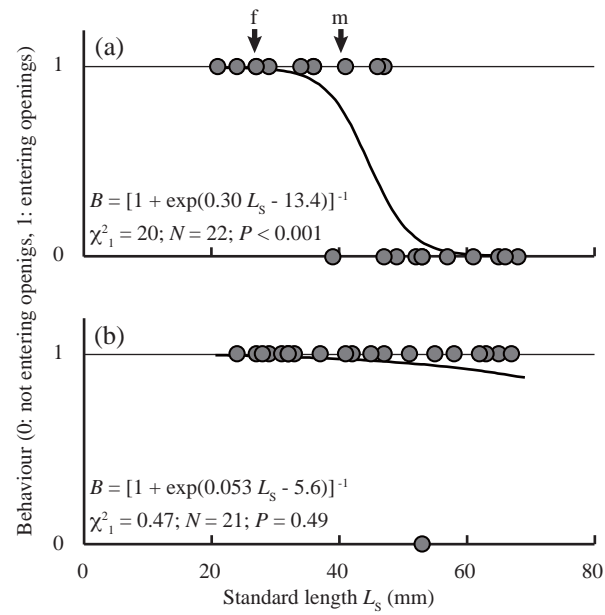


Fig. 4

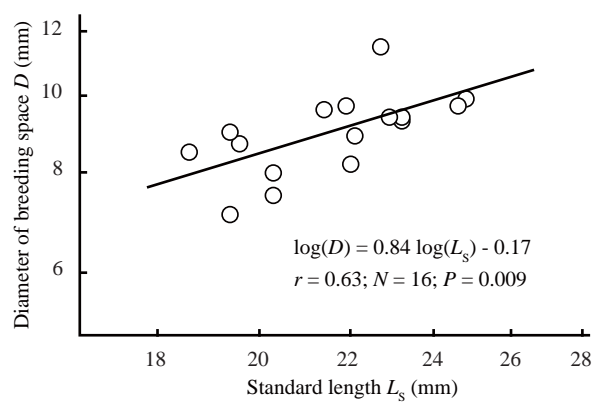


Fig. 5